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A new genus for *Pericera septemspinosa* Stimpson, 1871 and *Pericera heptacantha* Bell, 1836 (Crustacea, Brachyura, Majoidea), based on morphology and molecular data

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Abstract

A new genus of majoid spider crab, *Pohleus* **gen. nov.** is established for *Pericera septemspinosa* Stimpson, 1871 and *Pericera heptacantha* Bell, 1836, based on morphology and molecular data from the partial sequences of the 12S and 16S mitochondrial genes and the 18S small subunit rRNA nuclear locus. The species are re-described and illustrated, based on material from several localities of the western Atlantic and eastern Pacific oceans. The carapace, antennal and pterygostomial spines, male thoracic sternum and first gonopods are distinctive characters, distinguishing *Pohleus* **gen. nov.** from species assigned to *Macrocoeloma* Miers, 1879, where *P. septemspinosus* and *P. heptacanthus* are currently included.

Key Words

Epialtidae, Pisidae, western Atlantic, eastern Pacific, *Macrocoeloma heptacanthum*, *Macrocoeloma septemspinosum*

Introduction

Macrocoeloma heptacanthum (Bell, 1836) and *M. septemspinosum* (Stimpson, 1871) were originally described as *Pericera* Latreille, 1825 and transferred by Miers (1886) to *Macrocoeloma* Miers, 1879 (see Colavite et al. 2016 for review). As part of an ongoing revision of *Macrocoeloma*, we identified the necessity to establish a new genus for the above two species. The description of *Pericera heptacantha* was based on two syntypes, one male and one female. This type material was treated as missing in literature for more than 50 years (see Rathbun 1925; Garth 1958) until the female specimen was re-discovered by Di Mauro (1982) in the dry crustacean collection in the University Museum, Oxford (OUM). *Pericera septemspinosa*, from the western Atlantic, was described by Stimpson (1871) as a geographical analogue to *Pericera heptacantha* from the eastern Pacific and, unfortunately, the type material of *P. septemspinosa* was most likely destroyed in the Great Chicago Fire in 1871 (Evans 1967; Deiss and Manning 1981; Manning 1993; Vasile et al. 2005; Manning and Reed 2006).

Pohleus gen. nov., is proposed herein to receive *Pericera heptacantha* and *P. septemspinosa* and a lectotype and a neotype are designated for each species, respectively. The species are re-described, illustrated and the morphological differences between them are detailed below. A phylogenetic framework for *Pohleus* gen. nov. and allied genera is proposed, based on partial sequences of the 12S and 16S mitochondrial genes and the 18S small subunit rRNA nuclear locus.

Material and methods

Specimens examined are deposited in the collections of the Coleção de Invertebrados Aquáticos do Sul da Bahia, Universidade Estadual de Santa Cruz, Brazil (CIASB/UESC); Grupo de Invetigaciones Carcinologicas, Universidad de Oriente, Venezuela (GIC); Laboratório de Sistemática Zoológica, Universidade do Sagrado Coração, Bauru (LSZ); Muséum National d'Histoire Naturelle, Paris (MNHN); Museum of Comparative Zoology, Harvard University (MCZ); Museu de Zoologia da Universidade de São Paulo (MZUSP); Natural History Museum of Los Angeles County (NHMLA); Zoological collection of the Oxford University Museum of Natural History (OUM); Senckenberg Museum of Natural History, Frankfurt (SMF); University of Louisiana at Lafayette Zoological Collection (ULLZ) and the National Museum of Natural History, Smithsonian Institution (USNM). For comparisons between *Pohleus* gen. nov. and *Macrocoeloma* s. str., 11 of the 12 known species of *Macrocoeloma* were examined, including the type species *Macrocoeloma trispinosum* Latreille, 1825 (see Comparative material section below). Additionally, the monotypic genus *Thersandrus* Rathbun, 1897 (type species *Thersandrus compressus* (Desbonne in Desbonne & Schramm, 1867) was included in our comparisons.

Abbreviations used are: cl, carapace length (along the dorsal midline, from the base of the rostral sinus to the posterior margin of the carapace); cw, carapace width (taken at the widest point including lateral spines); P2–P5, pereopods 2 to 5 (P1 is the cheliped); G1, first gonopod; G2, second gonopod; ovig., ovigerous; juv., juvenile; RV, research vessel; exped., expedition; stn, station; leg., collector or collected by; det., determined by.

DNA extraction, PCR, and sequencing

Total genomic DNA was extracted from muscle tissue using either the Qiagen DNeasy Blood and Tissue extraction kit or Omega Bio-tek EZNA Tissue DNA Kit. Partial sequences of the 12S, 16S mitochondrial genes were amplified with the following primers, respectively: 12SF (Mokady et al. 1994) and 12S1R (Shull et al. 2005), 16SF/16SR (Hultgren and Stachowicz 2008). The nuclear loci of the small subunit 18S rRNA were amplified with the primers A and B (Medlin et al. 1988) and C, Y, O and L of Apakupakul et al. (1999) or D18s1R, D18s2F/R, D18s3F/R, D18s4F/R and D18s5F of Bracken et al. (2009). Annealing temperatures for PCRs were 58 °C and 54 °C for 12S/18S and 16S, respectively. Reagent volumes and concentrations followed manufacturer's instructions; primer concentrations were 10 µM. Sequencing reactions were performed using 1 µl of purified PCR product in a 10 µl reaction containing 0.5 µl primer, 1.75 µl BigDye buffer and 0.5 µl BigDye (Life Technologies). Sequencing reactions were purified using Millipore Sephadex plates (MAHVN–4550), according to the manufacturer's instructions and sequenced on the ABI 3730XL automated DNA sequencer. Sequences were assembled, trimmed of primers and checked for quality using Geneious 8.0.5 and 9.1.8. DNA extraction and sequencing were carried out at the Smithsonian Institution's Laboratories of Analytical Biology.

Molecular data analysis

Sequences, generated for this study, were combined with other sequences available from GenBank and previously unpublished sequences generated by AMW, in order to place the target taxa within the context of the superfamily Majoidea. Locality information and GenBank accession numbers for taxa included in the molecular analyses are provided in Suppl. material 1: Table S1. All individual sequences for each species were initially analysed and assembled using the software Geneious 8.0.5 (http://www.geneious.com; Kearse et al. 2012). The alignment amongst all sequences was generated with the algorithm Muscle (Edgar 2004) under default parameters and the perl script PartitionFinder (Lanfear et al. 2017) on CIPRES Portal (Miller et al. 2010) was run to determine the appropriate model of evolution and partitioning scheme. To determine whether the sequence data was appropriate for phylogenetic studies, the occurrence of substitution saturation was evaluated in the molecular data and identical sequences were excluded, resulting in 23 unique sequences. Numbers of transition and transversions versus ML-CompositeTN93 distance were plotted using the software DAMBE 7.2.7 (Xia 2013, 2017), with the options of pairwise deletion and genetic distance model F84. The individual datasets were concatenated in RAxML, where we used the '-f ae' option with 1000 bootstrap replicates. Likelihood parameters followed the General Time Reversible (GTR) model with a gamma distribution on the partitioned dataset and RAxML estimated all free parameters. The resulting best tree was used to reflect phylogeny (Fig. 1). To establish the phylogenetic context for *Pohleus septemspinosus* gen. nov. et comb. nov., we followed the previous phylogenies of Majoidea (Hultgren and Stachowicz 2008, 2009; Windsor and Felder 2014) to choose the genera used in this study and rooted the tree with the hymenosomatid crab *Elamena producta* Kirk, 1879. Only nodes with maximum likelihood bootstrap support greater than 50% are shown on the maximum likelihood phylogram (Fig. 1). All analyses were run on the Hydra computing cluster at USNM or CIPRES Portal (Miller et al. 2010). Nodes, where maximum likelihood bootstrap support is greater than 50%, are shown on the maximum likelihood phylogram (Fig. 1).

The ongoing revision and phylogenetic study of *Macrocoeloma* by the authors (unpubl. data), based on both morphological and molecular data, revealed this genus to be a paraphyletic group. *Pohleus* gen. nov. therefore, needs to be established to accommodate *P. septemspinosus* gen. nov. et comb. nov. and *P. heptacanthus* gen. nov. et comb. nov.

Results and discussion

All three genes (12S, 16S and 18S) were successfully amplified and sequenced only for *Pohleus septemspinosus* gen. nov. et comb. nov. The final alignment for this combined analysis of nuclear and mitochondrial genes included a total of 2659 bp (1868 bp 18S, 417 bp 16S and 372 bp 12S). The data were not saturated, considering the R^2 value for transitions R^2 (s) = 0.8665 and R^2 (v) = 0.9856 transversions, demonstrating that the sequences are appropriate for phylogenetic studies at this level.

Pohleus septemspinosus gen. nov. et comb. nov. has a high support value (84%) as sister to a clade containing *Thersandrus compressus* and *Macrocoeloma* spp. *Thersandrus*, presently assigned to the subfamily Majinae *sensu* Ng et al. (2008), is supported 89% as basal to *Macrocoeloma* and nested between *Macrocoeloma* and *Pohleus* gen. nov. in all scenarios analysed and with high support (Fig. 1). Thus, we believe that *Thersandrus* could be better fitted in Pisinae, based on the molecular results. *Pohleus* gen. nov. nested amongst other Pisinae as expected (Fig. 1).

Systematics

Family Epialtidae MacLeay, 1838
Subfamily Pisinae Dana, 1851

***Pohleus* gen. nov.**

http://zoobank.org/6FB44605-6302-44ED-8667-F4B321C21C11

Type species. *Pericera septemspinosa* Stimpson, 1871, by present designation.

Included species. *Pohleus septemspinosus* (Stimpson, 1871) gen. nov. et comb. nov. and *Pohleus heptacanthus* (Bell, 1836) gen. nov. et comb. nov.

Diagnosis. Carapace subglobose, covered by short velvet pubescence interspaced by dense rows of long, hooked and simple setae in all carapace regions. Carapace armed with strong spines, including seven sharp spines on posterior half: one short mesial metagastric, four long, strong, conical lateral spines (two in each branchial region) aligned with one cardiac spine and one intestinal spine; lateral spines longest, slightly directed upwards. Pterygostomial region with strong spines visible in dorsal view. Rostrum bifurcated, base elongated, fused, diverging abruptly forming a Y-shape, ending in acute tips. Pre-orbital spine strong, acute, directed upwards; post-orbital spine short, acute. Basal article of antenna with three spines, one tubercle, not visible in dorsal view. Cheliped long, merus armed with short spines or tubercles, granulated. P2 shorter than cheliped, dactylus much shorter than propodus. Thoracic sternal somite IV with lateral margins straight. Sternite VIII concealed by pleon in males. Male and female pleon with six somites not fused plus telson. Male telson tight-fitting into sterno-pleonal cavity, distinctly triangular. G1 slender, straight, with bilobed apex. G2 slender, straight, tapering distally, short about one fifth of G1 length.

Comparative material. *Libinia spinosa* H. Milne Edwards, 1834 – Brazil • 1 male, 1 female; Macaé, near Santana Archipelago, PITA stn 12 III (MZUSP 20271). *Macrocoeloma camptocerum* (Stimpson ,1871) – USA • 13 males, 7 females, 7 ovig. females; Sanibel Island, 26.440359N, 82.113705W, 0.54–11 m depth; Mar 1938; F A Chace Jr. leg. det. (MCZ 10191). *Macrocoeloma concavum* Miers, 1886 – Venezuela • 1 female; Costa de Falcon, UTM 378365 and 1358259; 27 Apr 2007 (GIC040). Brazil • 1 male; Paraíba, Projeto Algas, stn 85-B; 04 Jun 1981; Apr 2008, L E A Bezerra det. (MZUSP 5937). *Macrocoeloma diplacanthum* (Stimpson, 1860) – US Virgin Islands • 1 male; Saint Thom-

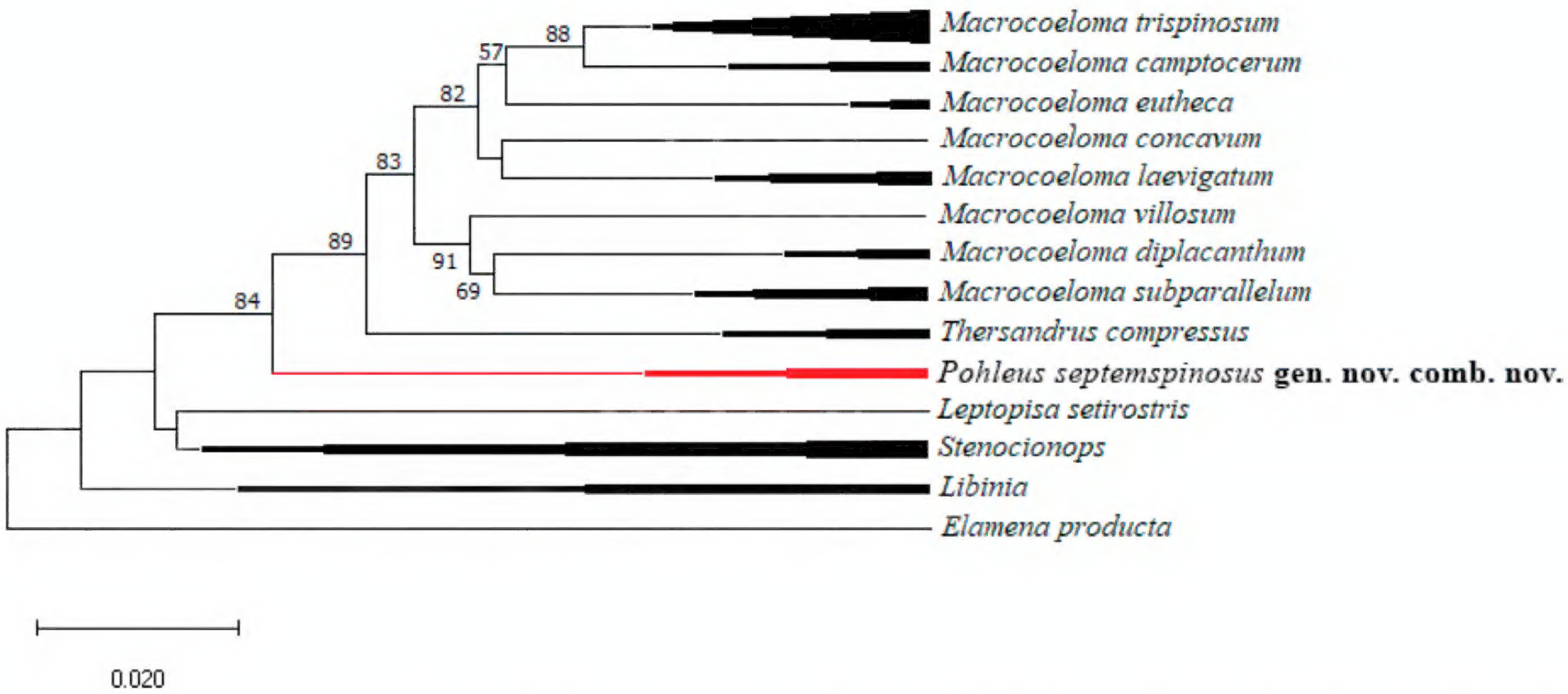

Figure 1. Molecular phylogenetic tree represented as maximum likelihood topology of two mitochondrial and one nuclear loci (12S, 16S and 18S) to place *Pohleus septemspinosus* (Stimpson, 1871) gen. nov. et comb. nov. based on six close genera. Nodal support values represent the frequencies observed, using 1000 bootstrap pseudo-replicates. Values below 50% are not represented.

as, R/V Albatross; 17–24 Jan 1884 (USNM 16182). Guadeloupe • 1 ovig. female; 16°13'37.3188"N, 61°32'23.0388"W, Karubenthos 2012, stn GD49; 21 May 2012 (MNHN IU-2013-6755). *Macrocoeloma eutheca*. (Stimpson,1871) – USA • 1 ovig. female; off North Carolina, 33°48'06"N, 76°34'42"W, 77 m depth; 03 Apr 1981; Duke University for MMS 0S05 exped., 1981, P Krikorian det. (USNM 220812). *Macrocoeloma intermedium* Rathbun, 1901 – Cuba • male holotype; off Havana, R/V Albatross, stn 2323, 23°10'51"N, 82°19'03"W, 298 m depth; 17 Jan 1885; M J Rathbun det. (USNM 9492). Colombia • 1 female; Santa Marta; 29 Jun 1975; M Vélez det. (SMF 9093). *Macrocoeloma laevigatum* (Stimpson, 1860) – USA • 1 male; Florida, Hawk Channel, R/V Fish Hawk, stn 7429, 4.2 m depth; 27 Jan 1903 (USNM 46933). Bahamas • 1 female; off Whale Cay, 23.7 m depth, 9 Jul 1904, F A Chace Jr. det. (MCZ 8927). *Macrocoeloma maccullochae* Garth, 1940 – Mexico • 1 male, 1 female; Isabel Island, Allan Hancock Pacific exped., R/V Velero III, stn 747-37, 18–32 m depth; 2 Apr 1937; W Schmitt leg., 1940; J S Garth det. (NHMLAC-AHF 372). *Macrocoeloma nodipes* (Desbonne in Desbonne & Schramm, 1867) – USA• 3 males, 2 females; Florida, Off Cape Sable, R/V Fish Hawk, stn 7351, 25°09'45"N, 81°18'35"W, 17 Dec 1902, 5.9 m depth (USNM 46922). Grenada • 1 male; Grand Anse Bay, 12°01'45.19"N, 61°45'21.29"W, 11 Nov 2012, L R L Simone, A P Dornellas, V S Amaral leg., 27 Nov 2019, J Colavite det. (MZUSP 40162). *Macrocoeloma subparallelum* (Stimpson, 1860) – US Virgin Islands • male lectotype; soft shell, cl. 13.98 mm, cw. 9.90 mm; St. Thomas, 18.345591N, 64.923613W, no date, A H Riise leg., 1860, W Stimpson det. (MCZ 1243). Brazil • 3 females; Porto da Barra, Salvador, left side, 24 Apr 2006, R Bispo, R Jhonsson, W Santana, F Faria leg., Apr 2008, G Melo det. (MZUSP 18626). *Macrocoeloma trispinosum* (Latreille, 1825) – USA • 1 ovig. female; Kingston Harbour; 1893; R P Bigelow leg., M J Rathbun det. (USNM 17959). Antigua • 1 male; English Harbour, Antigua-Barbados exped., 1918; University of Iowa State exped., M J Rathbun det. (USNM 72956). *Macrocoeloma villosum* (Bell, 1836) – Ecuador • 3 males, 1 female; Salinas, Walter Rathbone Bacon travelling Scholarship exped., stn 1, 2, 3; 12–14 Sep 1926; W L Schmitt leg., M J Rathbun det. (USNM 70942). *Thersandrus compressus* (Desbonne in Desbonne & Schramm, 1867) – Belize • 1 male; west Bay, 1.3 m depth; 09 Jun 1985 (USNM 1526077).

Remarks. *Macrocoeloma* Miers, 1879 s. str. is an amphi-American genus with 12 species. This genus is characterised by the pyriform or triangular carapace, densely covered by short, velvet-like setae; with well-developed bifurcated or parallel rostral spines; the eyes completely protected by the orbits when retracted; orbits composed by the pre-orbital and the post-orbital spines and one or two projections of the basal article of antenna forming a functional, laterally projected protective hood. Although some of these characters can be observed in *Pohleus* gen. nov., the new genus can be easily distinguished from *Macrocoeloma* s. str. by a unique combination of characters, which include: (i) carapace relatively more globose in *Pohleus* gen. nov. (Figs 2A–C, 3, 4) (vs. carapace subtriangular or pyriform in *Macrocoeloma*; Fig. 2E, F); (ii) carapace covered by short velvet pubescence interspaced by dense rows of long hooked and simple setae in all carapace regions in *Pohleus* gen. nov. (Fig. 2C) (vs. carapace densely covered by velvet pubescence with hooked setae in specific regions of the carapace in *Macrocoeloma*); (iii) basal article of antenna with small spines ventrally directed, not visible in dorsal view in *Pohleus* gen. nov. (Fig. 2B) (vs. with a long laterally-directed spine, between the rostral and pre-orbital spine, visible in dorsal view of *Macrocoeloma*, except in *Macrocoeloma diplacanthum*; Fig. 2F); (iv) pterygostomial region with a strong spine, laterally projected, visible in dorsal view in *Pohleus* gen. nov. (Fig. 2B) (vs. pterygostomial spines short, reduced or not visible in dorsal view in *Macrocoeloma*; Fig. 2F); (v) male sterno-pleonal cavity with no crest anteriorly in *Pohleus* gen. nov. (Fig. 2B); (vs. male sterno-pleonal cavity with a distinct crest anteriorly on thoracic sternite IV in *Macrocoeloma*; Fig. 2E); (vi) male sternite IV almost straight laterally in *Pohleus* gen. nov. (Fig. 2B) (vs. sternite IV deeply concave laterally in *Macrocoeloma*; Fig. 2E); (vii) episternites IV and V forming a continuous line with the sternite, slightly downward directed in *Pohleus* gen. nov. (Fig. 2B) (vs. episternites IV, V and VI upward directed in *Macrocoeloma*; Fig. 2F); and (viii) sternal sutures shallow in *Pohleus* gen. nov. (Fig. 2B) (vs. sternal sutures deep sculpted in *Macrocoeloma*; Fig. 2F).

In *Macrocoeloma*, the gonopods are highly variable amongst species, but it is possible to recognise a general pattern with G1 being longer than the thoracic sternal suture IV/V, parallel and usually with a bilobed apex (except in *M. concavum*, *M. intermedium* and *M. laevigatum* that have a unilobed apex). Although *Pohleus septemspinosus* gen. nov. et comb. nov. (G1 of *Pohleus heptacanthus* gen. nov. et comb. nov. not examined) can be fitted in this general pattern, the G1 apex is notably more similar to the G1 apex of *Libinia* Leach, 1815 (Fig. 2D and see Tavares and Santana 2011: 63, fig. 2D for *Libinia spinosa*).

Thersandrus Rathbun, 1897, is a monotypic genus exhibiting extremely efficient camouflage behaviour as *Macrocoeloma* and *Pohleus* gen. nov. However, *Thersandrus* does not actively decorate itself, presenting crypsis behaviour consisting of matching the body to the environment in shape and colour, being morphologically adapted to live on green algae fronds. For instance: (i) *Thersandrus* has a carapace covered by long setae giving a felt-like texture (vs. velvet-like and hooked setae in *Macrocoeloma* and *Pohleus* gen. nov.); (ii) the carapace

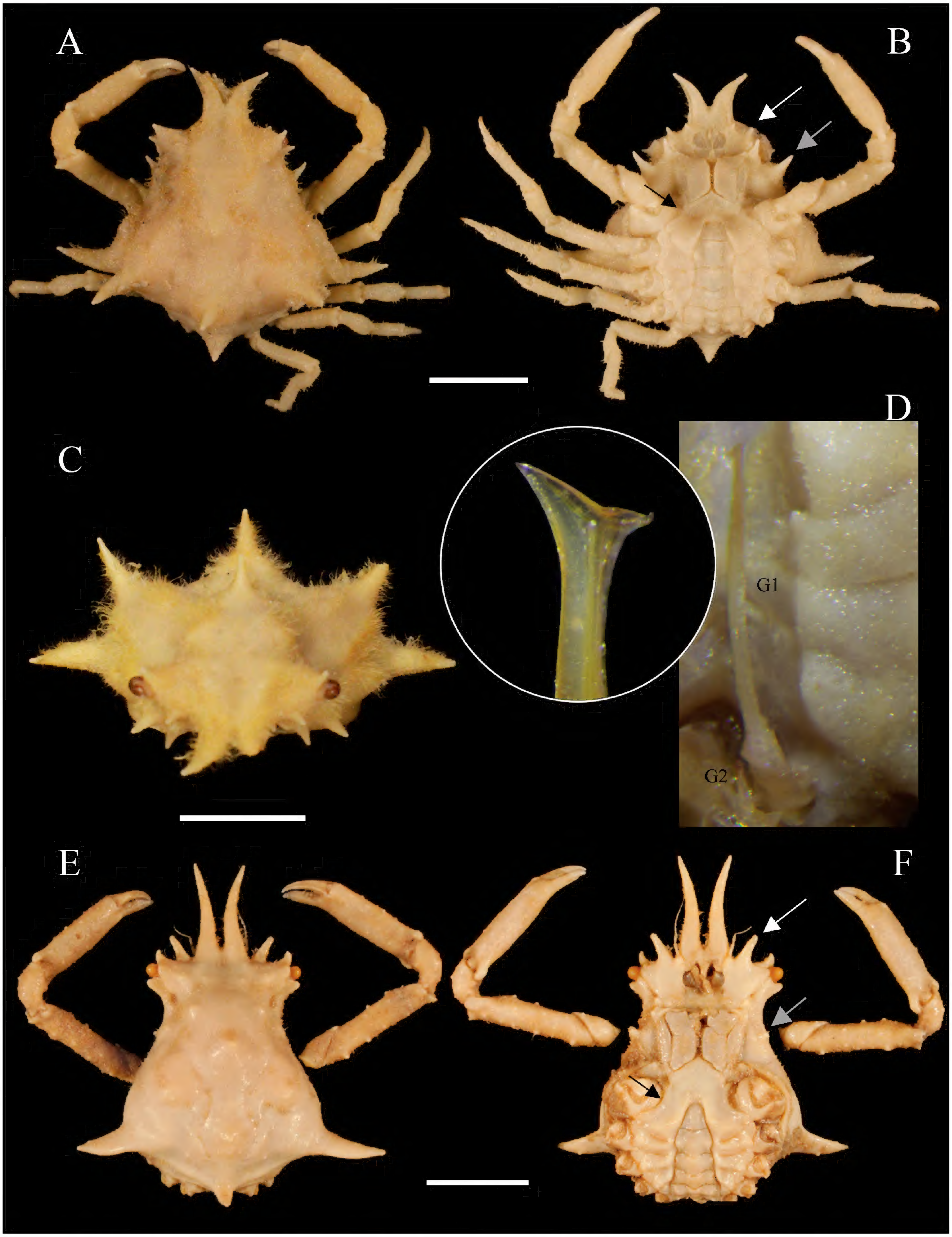

Figure 2. *Pohleus septemspinosus* (Stimpson, 1871) gen. nov. et comb. nov. **A, B.** male, (USNM 1256361); **C.** male (USNM 241030); **D.** sterno-pleonal cavity with first (G1) and second (G2) gonopods in place (USNM 1256361). *Macrocoeloma trispinosum* (Latreille, 1825); **E, F.** male (USNM 17959). **A, E.** habitus; **B, F.** ventral view; **C.** frontal view; **D.** pleonal view in detail. Note the spine of the basal article of antenna (white arrow); pterygostomial spine (grey arrow); margin of the IV sternite thoracic (black arrow). Scale bars: 10 mm.

and pereopods are flattened in *Thersandrus* (vs. carapace subtriangular or piriform, not flattened and with cylindrical pereopods in *Macrocoeloma* and subglobose carapace and cylindrical pereopods in *Pohleus* gen. nov.); (iii) the orbital spines are reduced, not forming a hood in *Thersandrus* (vs. orbital spines long, blunt, forming a hood in *Macrocoeloma* and long, acute and forming a hood in *Pohleus* gen. nov.); all characters that prevented us from synonymising *Thersandrus* to *Macrocoeloma*. However, it is important to note that, based on the molecular results, *Thersandrus* should be transferred from Majidae to Pisinae as mentioned above.

Etymology. Generic name in honour of the renowned marine biologist and carcinologist Gerhard Werner Pohle (Atlantic Reference Centre, Huntsman Marine Science Centre). Gender masculine.

Pohleus septemspinosus (Stimpson, 1871) gen. nov. et comb. nov.

Figs 2A–D, 3, 5A, B

Pericera septemspinosa Stimpson, 1870 (1871): 113 [type locality: West of Tortugas; 65 m depth, type material: non-extant]. – A. Milne-Edwards 1873: 59, 200, pl. 15A, fig. 2; Gundlach and Torralbas 1900: 365, fig. 366G.

Macrocoeloma septemspinosa – Miers, 1886: 80; Rathbun, 1892: 250; 1898b: 257; 1899: 576.

Macrocoeloma septemspinosum – Moreira 1901: 64, 136; Rathbun 1925: 477, pl. 173, figs 2, 3; Coelho 1971:142; Coelho and Ramos 1972: 218; Soto 1980 (digital document); Powers 1977: 52; Takeda and Okutani 1983: 141; Abele and Kim 1986: 45, fig. 521A; Melo 1996: 219, fig. 1; 1998: 464; Coelho-Filho 2006: 19; Almeida et al. 2007: 15; Alves et al. 2008: 58; Ng et al. 2008: 119; Alves et al. 2012: 54.

Neotype (Here designated).

USA • male neotype, cl 31 mm, cw 35 mm; Florida, West of Sarasota, R/V Oregon, stn 4088, 27°44'N, 83°45'W; 04 Dec 1962, National Marine Fisheries Service exped.; 27 Oct 2014, W Santana det. (USNM 1256361) (Fig. 2A, B, D).

Material examined. USA • 1 male; North Carolina, 33°48'06"N, 76°34'42"W, 77 m depth; 03 Apr 1981, Duke Univ. for MMS leg.; 1981, P Krikorian det. (USNM 220811). • 1 male, 1 juv. female; South Carolina, East of Cape Romain, R/V Albatross, stn 2311, 32°55'00"N, 77°54'00"W, 59.1°F, 114.4 m depth; 05 Jan 1885, U.S. fish commission leg. (USNM 15127). • 1 juv.; Florida, between Cedar Keys and Delta of Mississippi, R/ V Albatross, stn 2369–2374, 46–48 m depth; Feb 1885 (USNM 46957). • 1 juv. female; Gulf of Mexico, Southwest of Cape San Blas, R/V Albatross, stn 2373, 29°14'00"N, 85°29'15"W, 45.7 m depth; 07 Feb 1886 (USNM 15132). • 1 juv. female, 1 male; same collection data as preceding (USNM 15130). • 2 females; same collection data as preceding (USNM 15131). • 1 male; Suez of Mexico, R/V Oregon, stn 892, 28°55'N, 85°07'W, 53 m depth; 07 Mar 1954, Fish and Wildlife leg.; 21 Apr 1954, F A Chace Jr det. (USNM 96389). • 1 male; off Apalachicola Bay, R/V Indian Seal, 28°49'59"N, 85°37'02"W, 177 m depth; 31 Jan 1978; R Lemaitre det. (USNM 1085620). • 1 male; South of Dog Island, R/V Albatross, stn 2407, 28°47'30"N, 84°37'00"W, 43.8 m depth; 07 Feb 1886, U.S. fish commission exped.; M J Rathbun det. (USNM 15135). • 3 juv. females; South of stn George Island, R/V Albatross, stn 2406, 28°46'00"N, 84°49'00"W, 47.5 m depth; 15 Mar 1885 (USNM 15134). • 1 female; 26°45'52"N, 83°21'26"W, 50.2 m depth; 18 Jul 1981, Continental Shelf Associates exped.; R Lemaitre det. (USNM 273379). • 1 male; same collection data as preceding (USNM 241027). •1 juv. female; same collection data as preceding (USNM 236995). • 1 male; 26°16'50"N, 83°23'49"W, 55.5 m depth; 05 Feb 1982, Continental Shelf Associates exped.; R Lemaitre det., (USNM 241026). • 1 male, 2 females; same collection data as preceding (USNM 273381). • 1 female, 1 male; same collection data as preceding (USNM 241024). • 1 male, 1 ovig. female; same collection data as preceding (USNM 229838). • 1 male; 26°16'44"N, 83°42'49"W, 71.3 m depth; 03 Nov 1980, Continental Shelf Associates exped.; R Lemaitre det. (USNM 236994). • 1 juv. female; same collection data as preceding (USNM 241007). • 1 male; same collection data as preceding (USNM 236987). • 2 males; same collection data as preceding (USNM 236986). • 1 male; 26°16'43"N, 83°46'49"W, 77 m depth; 24 Jun 1981, Continental Shelf Associates exped.; R Lemaitre det. (USNM 241029). • 1 female; same collection data as preceding (USNM 273382). • 1 male; 25°45'35"N, 83°20'14"W, 58.5 m depth; 24 Apr 1981, Continental Shelf Associates exped.; R Lemaitre det. (USNM 242947). • 1 male; R/V Silver Bay, 25°32'N, 80°04'W, 65.8 m depth; 24 Oct 1960; Oct.1970, D J G Griffin det. (USNM 1278767). • 1 female; off Dry Tortugas, 24°34'N, 83°16'W, 65.8 m depth; Dec 1877- Jan 1878, USCSS Blake exped.; A. Milne-Edwards det. (MCZ 8206). • 1 male, 1 female; off Key West, R/V Albatross, 24°25'45"N, 81°46'45"W, stn 2317, 75 °F, 82.3 m depth; 15 Jan 1885, U.S. fish commission exped. (USNM 15128). • 1 male, 1 female; same collection data as preceding (USNM 15129). • 1 male; Off Key West, Sand key Light bearing West Northwest, Key West Light bearing North, State Univ. Iowa exped., stn 24, 109.7 m depth; 19 Jun 1893, M J Rathbun det. (USNM 75724). • 1 male; same collection data as preceding (USNM 72863). • 1 male, 1 juv. female; Sand Key Light bearing Northwest by North, Key West Light North 0.5mile East, 91.4–109.7 m depth (USNM 68913). • 1 male; Florida, Pompano; 23 May 1949 (AMNH 10961). Bahamas • 1 juv. female; Bahamas Bank; 18 May 1893, State Univ. Iowa Bahamas exped. (USNM 72862). Colombia, • 1 male; 2 miles Southwest of Cape La Vela; 8 Apr 1939, J Garth leg.; 17 Jan 2018, J Colavite det. (AHF 39295). • 1 juv. female; 2 miles off Bahia Honda, R/V Velero III, stn A15-39, 9–18.28 m depth; 08 Apr 1939, J Garth det. (AHF 39292). Venezuela • 1 juv. male; 7 miles of Tortugas Island, R/V Velero III, stn A43-39, 73–75 m depth; 21 Apr 1939, J Garth det. (AHF 39293). • 1 male; 125 miles northeast of Macaibo, 12°37'N, 70°45'W, R/V Oregon, stn 4400, 97 m depth; 26 Sep 1963; 27 Oct 2014, W Santana det. (USNM 1256370). • 1 male; 50 miles

northeast of Caracas, 10°44'N, 66°09'W, R/V Oregon, stn 4466, 73 m depth; 17 Oct 1963; 23 Oct 2014, W Santana det. (USNM 1256347). French Guiana • 1 ovig. female; Guiana 2014 exped., R/V Hermano Gines, 6°17'58.2"N, 52°13'18.5952"W, 95–97 m depth; 08 Aug 2014 (MNHN IU 2013-2682). Brazil • 1 ovig. female; Recife, dredge 2; J Colavite det. (R2 unnumbered). • 1 ovig. female; Bahia, Ilhéus, Costa de Ilhéus, 14°43'33"S, 38°57'20"W, 41–42 m depth; 28 Nov 2004, A O Almeida det.; old number MZUESC 406 (CIASB M. 2017.0084. UESC).

Diagnosis. Rostrum width half of interorbital length bifurcated, base elongated, fused, diverging abruptly forming a Y-shape. Pleonal somite II smooth; merus of second pereopod armed with a spine.

Description. Cephalothorax and appendages sparsely covered with short, velvet-like pubescence. Carapace subglobose wider than long, convex, with long lines of hooked and simple setae in all carapace regions, denser in rostral and lateral spines. Rostrum width half of interorbital length bifurcated, base elongated and fused, abruptly diverging forming a Y-shape, ending in acute tips. Interorbital region slightly depressed medially. Hepatic region broad. One metagastric spine. Four long, strong, conical lateral spines (two in each branchial region), in line with the cardiac spine. One short intestinal spine. Orbital region very prominent, eyes completely protected in orbit when retracted, ocular peduncle visible when not retracted. Pre-orbital spine acute, directed upwards, tip curved, longer than post-orbital spine, ventral margin of pre-orbital spine with a small crenulation; post-orbital spine curved upwards.

Antennular fossae wider than long, margins smooth. Interantennular septum elongated, compressed laterally, forming distinct, ventrally-directed lobe. First and second antennal articles fused to epistome, suture between antenna and epistome visible, antennal gland opening near suture line. Basal article of antenna with three spines, one tubercle, not visible in dorsal view. Antennal flagella longer than rostral spines, behind rostrum in dorsal view.

Epistome anterior margin narrower than antennular fossae, smooth. Buccal field sub-quadrate, narrower at posterior edge with acute spine at anterolateral angle in line with antennal spines. Third maxillipeds completely covering buccal field. Exopod long, nearly reaching distal margin of merus. Pterygostomial region subtriangular, slightly inflated, separated from subhepatic region by marked groove, one long, strong spine slightly curved upwards on medial margin, visible in dorsal view.

Chelipeds equal, longer than pereopods in adults, more robust in adult males; females chelipeds shorter than males, slender. In males, ischium, merus, carpus and propodus segments granulate. Ischium with one prominent tubercle laterodistally. Merus with one spine on proximal half, one on distal margin. Carpus with four tubercles sparsely distributed. Dactylus arched in adult males, a small gap between fingers, distinctly shorter than palm. Cutting edges with sub-equal teeth in distal half, one distinct proximal tooth in larger males; distal half with dark brown colour in fixed specimens. Female ischium, merus, carpus and propodus with smaller tubercles than males, dactylus slightly arched, without gap between fingers.

Pereopods short, slender, cylindrical. P2 longest, P3–P5 progressively decreasing in length. P2 merus with distinct spine in distolateral margin. Dactylus slightly curved, shorter than propodus, smooth ventrally, with corneous tip.

Male thoracic sternites I–IV fused, broadly triangular, smooth, anterior half declivous in ventral view, forming a carina along the sterno-pleonal cavity margin. Thoracic sternal somite IV with lateral margins straight. Telson fully fitted to cavity, anterior margin smooth. Sternite VIII

Figure 3. A. Habitus, dorsal view and **B.** ventral view of *Pohleus septemspinosus* (Stimpson, 1871) gen. nov. et comb. nov., female (R2 unnumbered). Colour in life with debris and algae for camouflage. Scale bars: 10 mm

concealed by pleon. Episternites IV and V forming a continuous line with the sternite, slightly downward directed.

Pleonal somites I–VI, telson free in males and females, slightly raised medially forming low longitudinal ridge. Male telson sub-triangular, apex rounded. Female pleon markedly arched, with row of setae marginally. Female telson transversally ovate.

G1 longer than thoracic sternal suture IV–V, stout, straight, parallel, with torsion in distal half, apex bilobed; mesial lobe short, with tip curved upwards; lateral lobe long, slightly arched, ending in an acute tip; lateral margin smooth. G2 slender, straight, very short (one fifth of G1 length), with disto-medial process.

Colour in life. Carapace light brown; cephalothorax ventral, pleon and pereopods pinkish to purple (Fig. 3).

Neotype locality. USA, Florida, west of Sarasota, 27°44'N, 83°45'W.

Geographic distribution. Western Atlantic: USA (from North Carolina); Gulf of Mexico; Bahamas; Venezuela and Brazil (from Ceará to Bahia) (Fig. 4).

Remarks. The type material of *Pericera septemspinosa* was probably lost in the Great Chicago Fire in 1871 (see Evans 1967; Deiss and Manning 1981; Manning 1993; Vasile et al. 2005; Manning and Reed 2006). The male (USNM 1256361) is here designated as neotype of *Pericera septemspinosa* Stimpson, 1871 due to the close morphological similarity to the original description. The neotype is from a region close to the type locality. The specimen chosen here is from west of Sarasota, 27°44'N, 83°45'W (cf. ICZN art.75 and 76).

Pohleus septemspinosus gen. nov. et comb. nov. can be distinguished from its Pacific congener, *Pohleus heptacanthus* gen. nov. et comb. nov., by the following characters: (i) rostrum width half of the interorbital length in *P. septemspinosus* gen. nov. et comb. nov. (vs. rostrum with one-third or less of the interorbital length in *P. heptacanthus* gen. nov. et comb. nov.; Fig. 5C, D); (ii) pleonal somite II smooth in *P. septemspinosus* gen. nov. et comb. nov. (vs. pleonal somite II with one spine or tubercle in *P. heptacanthus* gen. nov. et comb. nov.; Fig. 5C, D); (iii) merus of the second pereopod armed with a spine in *P. septemspinosus* gen. nov. et comb. nov. (vs. merus of second pereopod unarmed in *P. heptacanthus* gen. nov. et comb. nov.; Fig. 5C, D). Unfortunately, no male specimens of *Pohleus heptacanthus* gen. nov. et comb. nov. were available for study, thus, the gonopodal differences cannot be ascertained.

The southeast record of this species as Espírito Santo State, in Brazil (Serejo et al. 2006: fig. 8C) is not valid, since the specimen (MNRJ 17062) was re-identified as *Macrocoeloma concavum*. Therefore, the distribution of to *Pohleus septemspinosus* gen. nov. et comb. nov. is corrected to the Brazilian coast, from Ceará to Bahia.

Pohleus heptacanthus (Bell, 1836) gen. nov. et comb. nov.

Fig. 5C, D

Pericera heptacantha Bell, 1836: 173 [type locality: Puerto Potrero, Central America, 23.7 m depth; type material: syntypes, 1 male (non-extant), 1 female (OUM 13764)] – Bell 1836b: 61, pl. 12, fig. 6 and 6r-u; White 1847: 10; A. Milne-Edwards 1873: 55.

Macrocoeloma heptacantha – Miers 1886: 79, 81.

Macrocoeloma heptacanthum – Rathbun 1898a: 576; 1925: 473, pl. 173, fig. 1; pl. 269, fig. 8–11, text-figs 133, 134; Garth 1958: 415; Di Mauro 1982: 170; Ng et al. 2008: 119.

Lectotype (Here designated).

Costa Rica • 1 female, cl: 35 mm, cw: 43 mm; Central America, Puerto Potrero, 23.7 m depth; H Cumming leg. (OUM 13764) (Fig. 5C, D).

Material examined. Mexico • 1 juv. female; Off Cape San Lucas, R/V Albatross, stn 2829, 22°52'00"N, 109°55'00"W, RKY leg., 56.6 m depth, 74.1 °F; 01 May 1888, M J Rathbun det. (USNM 21933 illustrated). Panama • 1 juv. female; Panama Bay, R/V Albatross, stn 2798, 8°10'30"N, 78°50'30"W, 114.6 m depth; 05 Mar1888, M J Rathbun det. (USNM 21932).

Diagnosis. Rostrum width less than one-third of interorbital length, bifurcated, base elongated, fused, diverging abruptly forming a Y-shape, ending in acute tip. Pleonal somite II with one spine or tubercle. Merus of second pereopod smooth.

Description based on female lectotype (male characters modified from Bell 1836b). Cephalothorax and appendages slightly covered with short, velvet-like pubescence. Carapace subglobose wider than long, convex, with long lines of hooked and simple setae in all regions. Rostrum short, less than one-third of interorbital length, bifurcated, base elongated, fused, diverging abruptly forming a Y-shape, ending in acute tips. Interorbital region slightly depressed medially. Hepatic region broad. One metagastric spine. Four long, strong, conical lateral spines (two in each branchial region), in line with cardiac spine. One short intestinal spine. Orbital region very prominent, eyes completely protected when retracted, ocular peduncle visible when not retracted. Pre-orbital spine directed upwards, slightly curved on tip, longer than post-orbital spine, ventral margin of pre-orbital spine with small crenulation; post-orbital spine curved upwards.

Antennular fossae wider than long, margins smooth. Interantennular septum elongate, laterally compressed, forming distinct ventrally-directed lobe. First and second antennal articles fused to epistome, with suture between antenna and epistome visible, antennal gland opening near suture line. Basal article of antenna with two spines, not visible in dorsal view: proximal spine smallest. An-

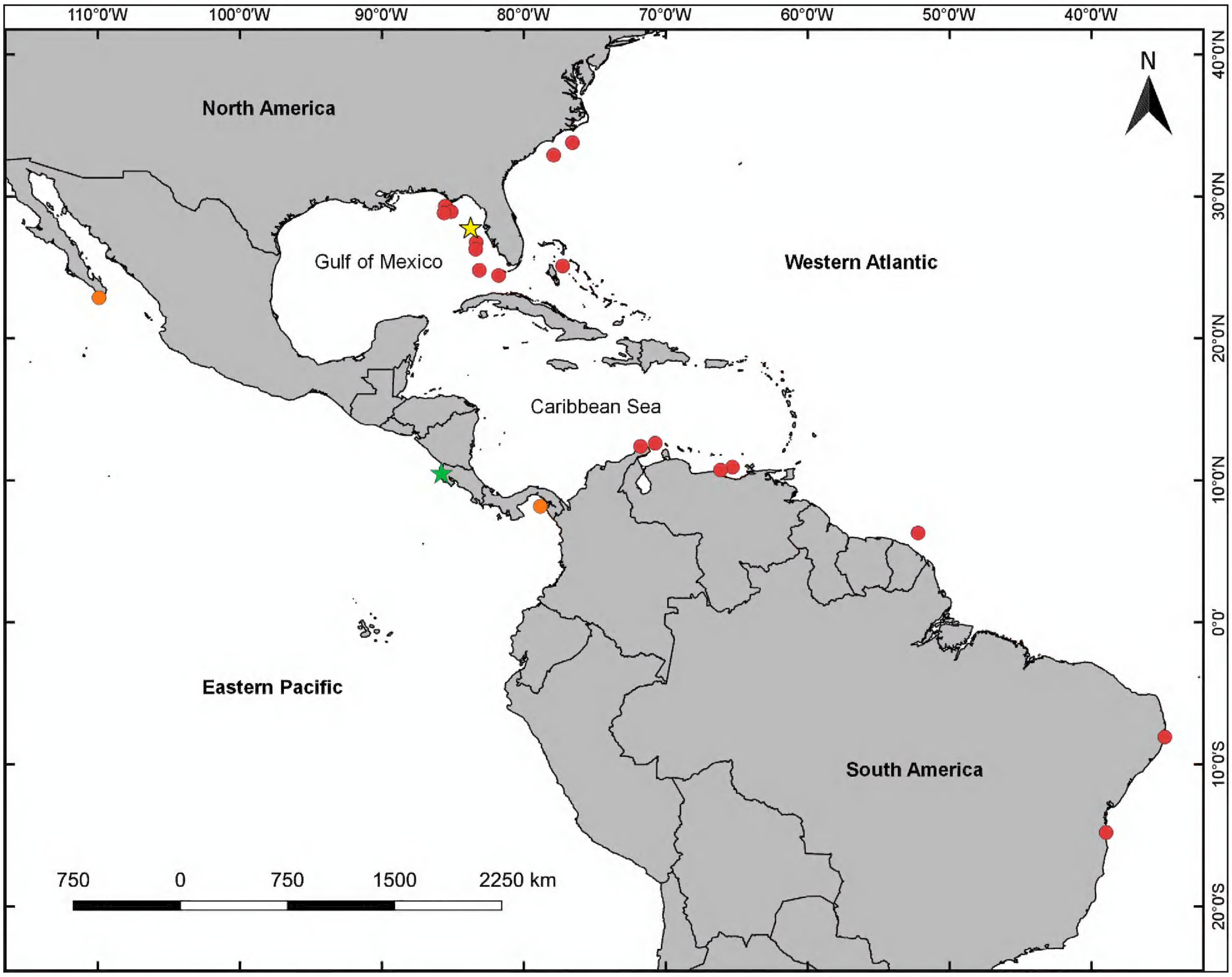

Figure 4. Geographic distribution *Pohleus heptacanthus* (Bell, 1836) gen. nov. et comb. nov.; orange circles = distribution based on examined material; green star = type locality and *Pohleus septemspinosus* (Stimpson, 1871) gen. nov. et comb. nov.; red circles = distribution based on examined material; yellow star = neotype locality.

tennal flagella longer than rostral spines, behind rostrum in dorsal view.

Epistome anterior margin narrower than antennular fossae, smooth, posterior margin slightly depressed. Buccal field sub-rectangular, narrower at posterior edge with one acute spine in anterolateral angle aligned with antennal spines. Third maxillipeds covering buccal frame when closed, leaving a small gap between ischia. Exopod long, nearly reaching distal margin of merus. Pterygostomial region subtriangular, slightly inflated, separated from subhepatic region by marked groove, with one long, strong spine slightly curved upwards on medial margin, visible in dorsal view.

Male chelipeds equal, longer than pereopods; covered with sparse granulation, unarmed. Dactylus arched in adult males, leaving small gap between fingers, distinctly shorter than palm. Cutting edges with sub-equal teeth in distal half, one distinct proximal tooth in larger males; distal half with light brown colour in fixed specimens. Pereopods short, slender, cylindrical. P2 longest; P3-P5 progressively decreasing in length. Dactylus slightly curved, covered with short setae.

Female chelipeds equal, longer than pereopods, slender and smooth. Dactylus arched in adult, shorter than palm, sub-equal teeth in distal half. Pereopods, slender, cylindrical. P2 longest, P3-P5 progressively decreasing in length. Dactylus slightly curved, shorter than propodus, smooth ventrally, with corneous tips.

Male thoracic sternites I–IV fused, broadly triangular, smooth, anterior half declivous in ventral view. Telson fully fitted to cavity, anterior margin smooth.

Female pleonal somites I–VI markedly arched, telson free, transversally oval, with a row of setae on margin and one small spine in first somite. Male pleon rather prominent, pleonal somites I–VI, telson free, somite II with a mesial tubercle. Somite III with slight elevations. Somite VI longest, with a mesial tubercle and a small projection each side.

Colour in life. Light brown, covered with darker hair, first pair of pereopods reddish (Bell 1936b).

Figure 5. *Pohleus septemspinosus* (Stimpson, 1871) gen. nov. et comb. nov. **A, B.** female (MNHN IU 2013-32682). *Pohleus heptacanthus* (Bell, 1836) gen. nov. et comb. nov.; **C, D.** female lectotype (OUM 13764). **A, C.** habitus; **B, D.** ventral view. Note the spine on merus of the second pereopod (white arrow). Scale bars: 10 mm.

Type locality. Costa Rica, Central America, Puerto Potrero, in sand at a depth of 23.7 m.

Geographic distribution. Eastern Pacific: Mexico (Cape San Lucas), Costa Rica (Guanacaste) and Panamá (Panama Bay) (Fig. 4).

Remarks. Bell (1836) described *Pericera heptacantha*, based on two specimens as syntypes, one male and one female. The male syntype is considered lost and the female is deposited in the dry crustacean collection of the Oxford University Museum (OUM 13764) (Di Mauro 1982). Thus, the female syntype (OUM 13764) is here designated as the lectotype of *Pericera heptacantha* since it is the only specimen from the type series remaining (Fig. 5C, D). The locality Puerto Potrero in Central America probably refers to the Puerto Potrero, Guanacaste, in Costa Rica. Rathbun (1937: 136) examining *Lithadia cumingii* Bell, 1855, a species described from the same locality by Bell (1855), referred to the type locality as from Potrero, Costa Rica, the same case as for *Pohleus heptacanthus* gen. nov. et comb. nov.

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Supplementary material 1

Table S1

Authors: Jessica Colavite, Amanda M. Windsor, William Santana

Data type: Species data

Explanation note: Taxa included in the molecular phylogenetic analyses to place the newly described taxa within the context of the family Pisidae.

Link: https://doi.org/10.3897/zse.96.50360.suppl1